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Mechanical adjustment of the suaharo (Cereus giganteus) to varying quantities of stored water

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(WITH PLATES 3 AND 4)

Among the desert plants of the southwestern United States that are provided with a well-developed system for water-storage, certain cacti, particularly those of columnar form, are conspicuously fluted with strong ribs and corresponding furrows that extend from base to apex of the stem. This structure naturally suggests a ready adjustment of the plant, by a bellows-like action of its ribs and furrows, to changes in bulk due to varying amounts of stored water. It is obvious, however, that such an adjustment, if it satisfies the requirements of successful adaptation, must not impair the efficiency of the general mechanical system; since these plants, rising like a columnar water-tank, often to the height of 50 or 60 feet, from a narrow base, are subjected to the force of high winds from every point of the compass.

To ascertain whether this bellows-like action actually takes place, a series of measurements and observations were undertaken at the Desert Laboratory during the winter of 1903–4. These were begun by the resident investigator, Dr. W. A. Cannon, and, at his suggestion, were afterwards carried out and extended by myself.

An inspection of a cross-section of the stem of a giant cactus will show a heavy band of thick-walled subepidermal tissue, which is exceedingly strong and elastic. Beneath this is a band of thin-walled chlorophyl-cells, and all the tissue between this and the

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ring of fibro-vascular bundles is made up of thin-walled water-storing cells.

From the construction it seems evident that a change in bulk corresponding to varying quantities of water contained in this tissue could hardly affect the central mechanical cylinder; but would be far more likely to manifest itself externally by expansion or contraction of the circumference, effected by folding or unfolding of the ribs and furrows.

To determine whether this actually takes place, measurements were made by marking with India ink points opposite each other on adjacent ribs, and, by means of callipers, measuring the distance between them at intervals of a day or more. Opposite points at the bases of the ribs were also marked in the same way, and the thickness of the ribs between these points measured by callipers. Finally a wire was placed around some of the plants, with a coiled spring, partially stretched, inserted between its ends. Variation in the length of the spring thus indicated any change that took place in the circumference. It was found that these three sets of measurements always corresponded. The ribs and furrows expanded and contracted at the same time, and their action was coincident with a corresponding increase or decrease in the circumference. For the sake of convenience, the comparisons which follow will be restricted to the measurements of the furrows.

To exhibit their changes graphically, curves were constructed, distances between ribs being laid off on the vertical axis, each space representing $\frac{1}{64}$ inch, and time being represented on the horizontal axis, each space representing one day. (In the accompanying diagrams every fifth line only is shown, so that each vertical space represents $\frac{5}{64}$ inch, and each horizontal space 5 days.) The English instead of the metric scale was employed, merely because the finest rule available at the time was in the former system. The measurements were all made with blunt callipers, and often when the cacti were swaying in the wind, so that absolute accuracy to $\frac{1}{64}$ of an inch was not always attainable; for all the comparisons made, however, it is believed that the curves are substantially correct.

The changes in width which the furrows exhibited will readily be understood from the curves constructed from measurements of

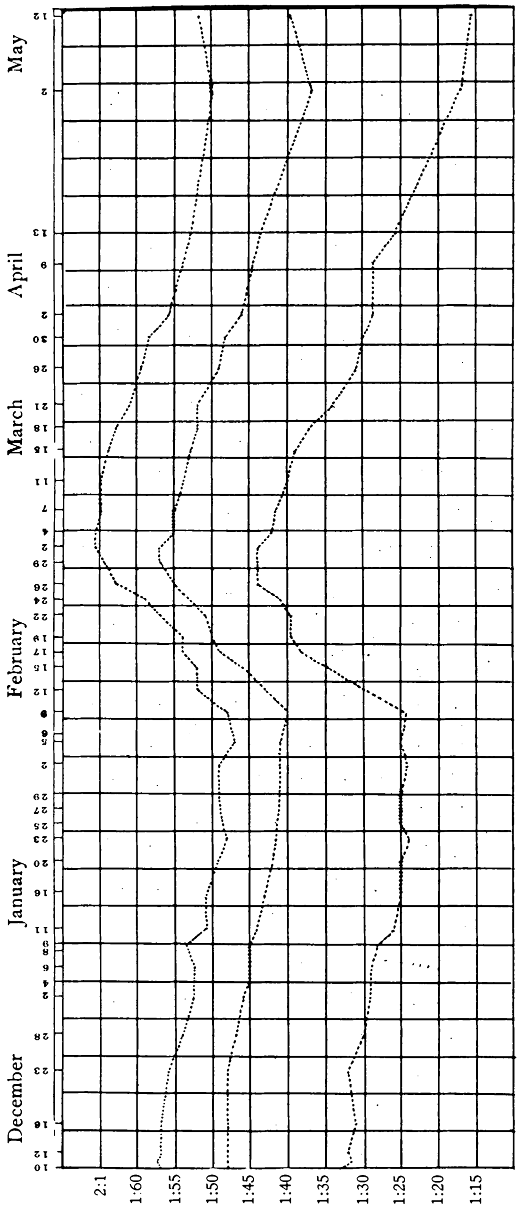

FIGURE 1. Curves derived from measurements of suaharo number 1. Rain, January 8 (0.2 in.), February 6 (0.54 in.), and May 2 (1 in.). The other days mentioned are the ones on which measurements were taken. In this and the following diagrams, each vertical space represents $\frac{5}{64}$ inch, and each horizontal space 5 days.

suaharo number 1 (*figure 1*), which may be regarded as in most respects a typical individual. This plant (*plate 3*) was about 12 feet high, in good condition, and the observations upon it were begun earlier and continued longer than on any other, thus covering more varied conditions than in any other case. The furrows marked were all on the north side, the points selected for measurement being about halfway from the ground to the top of the plant; and consequently the curves constructed from these measurements show a much greater similarity than those for which the measurements were made at different heights and on different sides.

The observations were begun December 10. During the cold, dry weather which followed, the edges of the furrows slowly approached, one of them losing $\frac{10}{64}$ of an inch in width. On February 6 there was a rain of 0.54 of an inch,* and this was followed by warmer weather. After this rain, the furrows expanded rapidly for nearly a month. This period was probably prolonged somewhat as a result of some water being poured out near the plant in the latter part of February. About March 2 the furrows began to grow narrower, and this continued during the warm, dry weather of March and April. On May 2 and 3 there was a rain of about one inch and slight expansion of two furrows followed. It is not known whether this expansion continued, as the observations were now brought to a close.

Inspection of the curves shows at a glance that expansion and contraction of the stem, indicated by varying distances between adjacent ribs, is correlated with water-supply; a conclusion abundantly confirmed by observations upon other individuals, especially numbers 2 and 9, which were furnished with water from artificial sources.

Number 2 was situated about eleven feet from the end of the pipe that carried off the waste water from the laboratory, and the slope of the ground was such that the water flowed close around its base. On March 12 this was changed, a trough carrying the water past the plant and emptying it on the slope below, though some water still probably reached the roots of the plant through leakage of the trough.

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*The statements as to amount of rain are all based on the records kept at the University of Arizona, some three miles from the Desert Laboratory, and 200 feet below it.

The first observations on this plant were made some three months after the opening of the laboratory, and judging from its full appearance and from other experiments, it is probable that the first effect of the water had been to cause an expansion of the stem. By the time observations were begun this had entirely ceased, but, as will be seen, it is evident that the presence of water in the soil was still exerting an influence. From January 9 to February 6, while the furrows of number 1 contracted $\frac{6}{64}$, $\frac{5}{64}$ and $\frac{4}{64}$ of an inch, two furrows of number 2 contracted only $\frac{1}{64}$ and a third $\frac{4}{64}$ of an inch (*figure 2*). The difference in the effect of the rain of February 6 was even more marked. While the furrows of number 1 showed an increase of $\frac{17}{64}$ to $\frac{20}{64}$ of an inch, those of number 2 only increased $\frac{6}{64}$ to $\frac{7}{64}$ of an inch, indicating that previous to the rain the cells of number 2 were much nearer their limit of expansion than those of number 1. It is evident then that the plant was able to avail itself to a considerable extent of the waste water of the laboratory, notwithstanding the large quantity of alkaline salts and other chemicals carried by it; and this is farther shown by its behavior after the period of expansion had ceased. Up to March 26, when the other cacti had been contracting for over

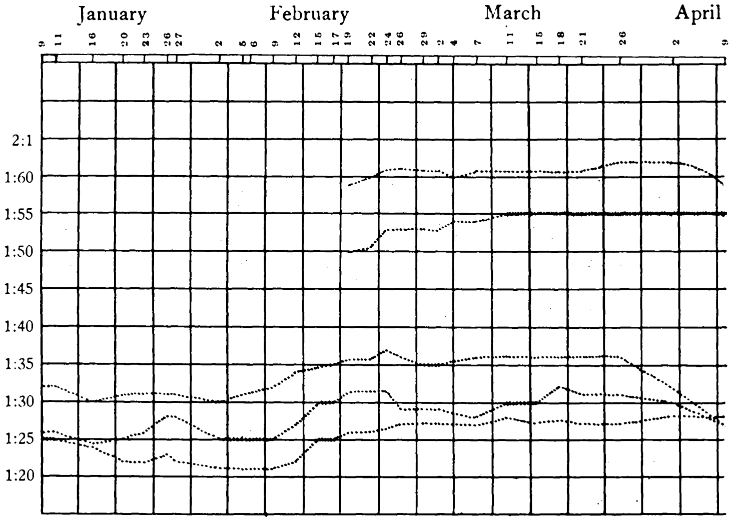


FIGURE 2. Curves for suaharo number 2. The measurements from which the three lower curves were derived were made on comparatively young branches, those for the two upper on lower and older parts of the stem. Rain, February 6 (0.54 in.).

three weeks, number 2 remained practically stationary. After this, two of three furrows that were marked shrank; but it was now receiving very little water.

The correlation of the expansion and contraction of the stem with its water-supply is demonstrated still more clearly by the measurements of another individual designated as number 9. On February 15, when the cacti under observation were all in process of expansion, this plant was selected and watered in order to ascertain whether by this means the period of expansion could be prolonged. Until March 4 it was given 8 to 12 gallons of water three times a week; after that, it was watered once a week until April 13. The water used was the ordinary tap-water charged with alkaline salts.

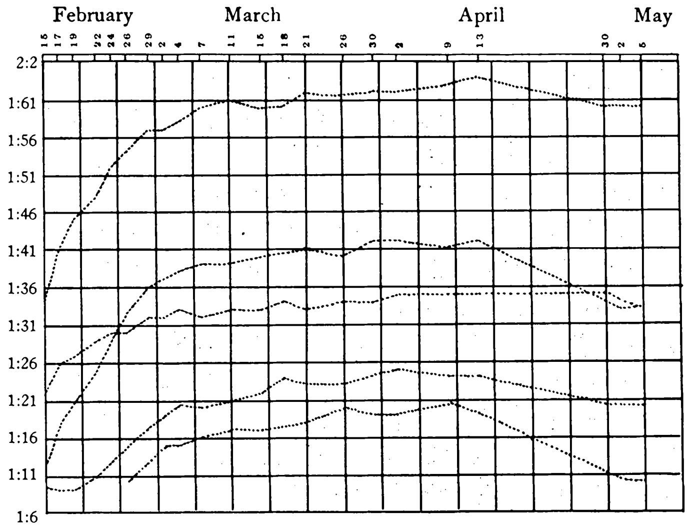


FIGURE 3. Representative curves derived from measurements of suaharo number 9. The lowest curve represents the variations in the thickness of a rib.

The behavior of the plant is shown by the curves in *figure 3*. It expanded very rapidly until about March 11, from one to three weeks after the other cacti had begun to contract. From then until between April 9 and 13 the furrows remained at about the same width while those of the others, except number 2, were contracting, some of them quite rapidly.

During this time, however, one cactus, number 4, accidentally received a thorough wetting by overflow and subsequent leakage from the water tank. It immediately stopped contracting, and in the next few days all the furrows marked expanded from one sixty-fourth to ten sixty-fourths of an inch (*figures 8* and *9*, *curve 4*.) After the soil had dried the furrows again contracted.

Nothing could show more clearly the relation between water-supply and the expansion and contraction of the trunk of the giant cactus than a comparison of the behavior of these artificially watered plants and that of number 1. Some idea of the limit of expansion can be gained from number 9, which after expanding for about five weeks, remained nearly stationary for a month, though the plant was well watered once a week. This would also indicate that the expansion which took place was the result of the absorption of water by the water-storing cells of the plant, and is not to be referred to growth.

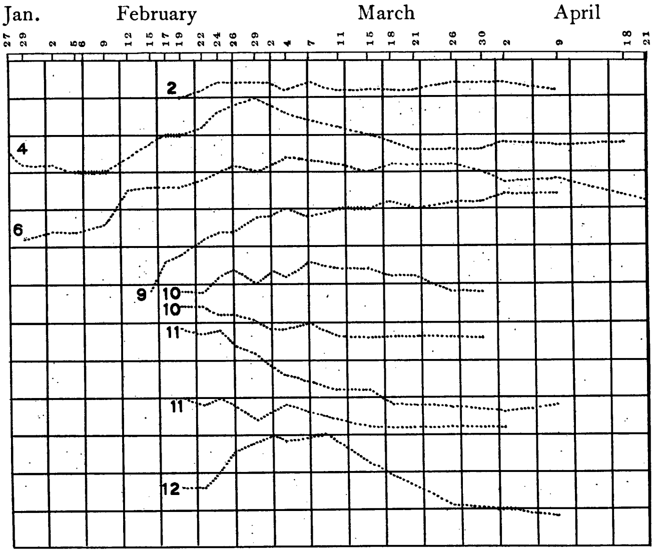


FIGURE 4. Curves derived from measurements near the bases of different plants. In this and the last two figures, in order to avoid confusion, the width of the furrows was ignored in placing the curves on the metric paper; and the figures refer to the number of the plant from which the curve was derived. Rain, February 6 (0.54 in.).

The other suaharos that were measured—designated 6, 7, 10, 11, 12—agree substantially with what has already been stated regarding number 1. Two bisnagas—numbered 5 and 8—showed the same phenomena as the suaharos, but on a smaller scale.

During the observations, it became evident that while the plant as a whole responded in the way described to variations in its water-supply, different parts of the stem were affected in different degrees, and to such an extent that one furrow might even be contracting while another on the same plant was expanding. These facts are most evident from the records of plants that were not watered.

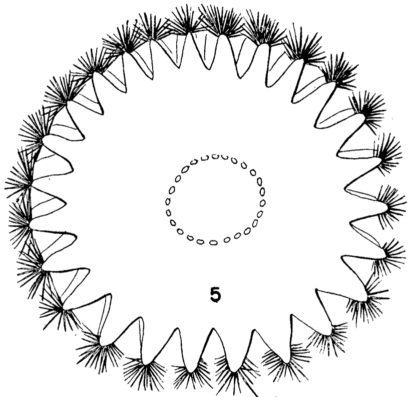
The lowest points at which measurements were made always showed a slow rate of change, and for a few inches below the apex the width of the furrows was stationary. Although observations were not sufficient to demonstrate any law as to comparative rate of change in different parts of the stem, a comparison of the curves in *figure 4* with those of any other set given will show that the variation near the base is less than higher up on the trunk.

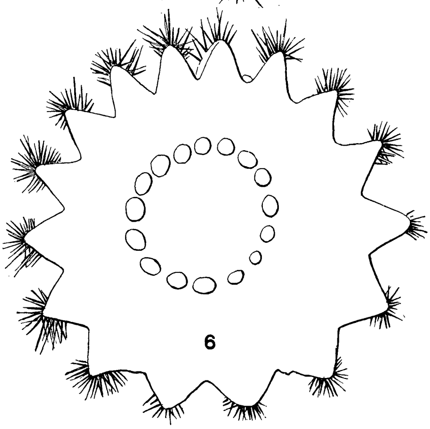
This difference in the rate of change at various heights of the stem is no doubt mainly due to the different proportion of mechanical and water-storing tissue as shown in *figures 5, 6* and *7* representing sections taken at 8 feet, 5 feet, and 15 inches from the base of a plant 9 feet high, but the different consistency of the cell-contents in the upper and lower parts of the stem may also be a factor.

The fact that no two furrows on the same stem vary exactly alike, even when measured at the same height, may also be understood by reference to the same figures. The contour of the sections shows that, beginning at the top, where the furrows are nearly equal all around the stem, their width and depth on opposite sides differ more as we pass to the lower portions. The deeper and narrower furrows are on the south; and the wider, shallower ones on the north side of the stem; and as we pass down to the suberized tissue near the base of the larger individuals the furrows all become obliterated and the ribs are finally marked only by rows of spines.

A comparison of the measurements from the north and south sides of the same plants (*figures 8* and *9*) shows that contraction is greater on the south than on the north side, and that while the southern furrows may begin to expand earlier, the northern ones expand longer. This difference in action of the two sides corresponds with the configuration of the mature stem, and suggests an interesting inquiry regarding the combined influence of temperature and light in the production of the form in question. To ascertain this and to find to what extent temperature as a secondary factor is active in the expansion and contraction of the stem would require observations extending over several seasons.

It will be instructive, however, to compare the curves already discussed with the temperature record for a corresponding period. From January 8 to 14 the mean temperature ranged from 42° to 56° F., and the effect of a rain of 0.2 of an inch was scarcely perceptible. From February 6 to 24 the mean temperature ranged from 47° to 68° F. and after a rain of half an inch the stems expanded steadily for three weeks. Later than this the mean temperature continued to increase during the period of observation, but, as already seen, the stems steadily contracted. It is noticeable, however, in comparing *figures 8* and *9*, that the furrows on the south side responded to the rain earlier than those on the north.





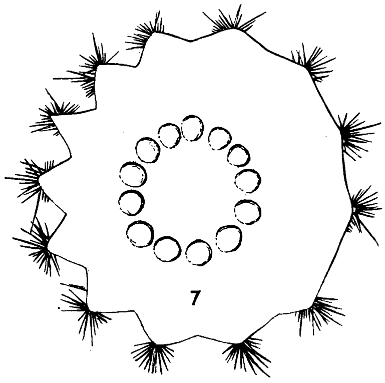


FIGURE 5. Section about 8 feet from the base, through the greatest diameter of the stem.

FIGURE 6. Section five feet from the base.

FIGURE 7. Section 15 inches from the base. The thin-walled, water-holding tissue becomes discolored almost immediately on contact with the air.

This very incomplete evidence indicates, as far as it goes, that temperature is an altogether subordinate factor, the effect of which, however, may increase or diminish that of water-supply.

Recurring again to the relation of the mechanical system to the processes of expansion and contraction, it would be difficult to imagine a more perfect arrangement for prompt and safe accommodation to variation in the large quantities of water held by these great columnar reservoirs. The strong central cylinder of fibrovascular bundles necessarily retains the relative position of its elements through all such variations; and the peripheral band of mechanical tissue is so disposed as to promptly adjust itself, by the simple change of position that has been described, to changes in the bulk of the tissue which it surrounds. The circumference of the stem can therefore be increased or diminished without interfering in the slightest degree, as far as the present observations indicate, with the strength or efficient distribution of either the central or peripheral mechanical elements. That the change in girth may be considerable in a relatively short period is shown by the fact that some furrows of number 9, which was watered about two months, actually increased 35 per cent. of their original width, and that one furrow on a plant not watered expanded

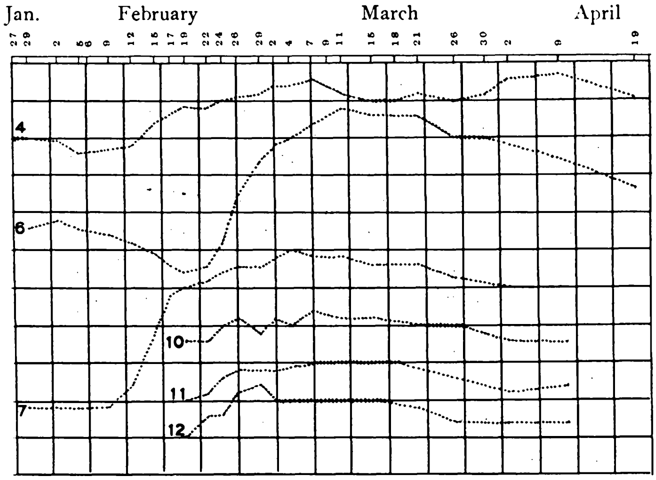


FIGURE 8. Six curves from as many different plants, each representing the variations of the furrow which faced nearest north. Rain, February 6 (0.54 in.).

one-half an inch in ten days after the rain of February 6 (*figure 9, curve 7*).

To summarize briefly, the foregoing observations lead to the following results:

1. Changes in the circumference of the stem of the suaharo are accomplished by a bellows-like action of the ribs, which draw closer together as the circumference decreases, and move farther apart as it increases.

2. These movements are directly correlated with increase and decrease in the water supplied to the plant, and with corresponding changes in the quantity of water held by its storage tissue.

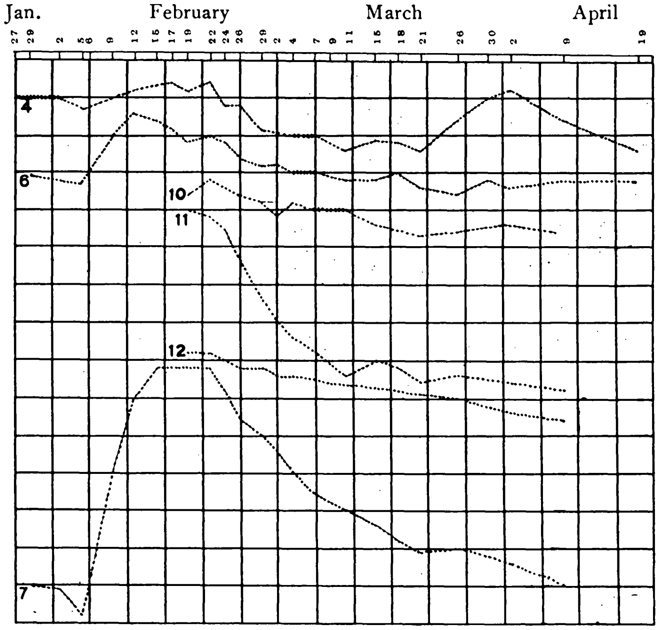


FIGURE 9. Six curves from the furrows facing nearest south on the same plants. The curves marked 4 in this figure and the preceding show the variation caused by an overflow of the water tank on March 18. Rain, February 6 (0.54 in.).

3. Variations in the circumference of the stem, due to changes of water-content, are not the same at all heights, but are least pronounced at the base and top.

4. In their expansion and contraction, the furrows on the north and south sides vary at different rates, which correspond with a difference in the configuration of the two sides.

5. Changes in the circumference of the stem effected by the mechanism described, while permitting free expansion and contraction of the water-storing tissue, leave the efficiency of the mechanical system unimpaired through all the vicissitudes to which the plant is subjected, and which it resists with a remarkable degree of success.

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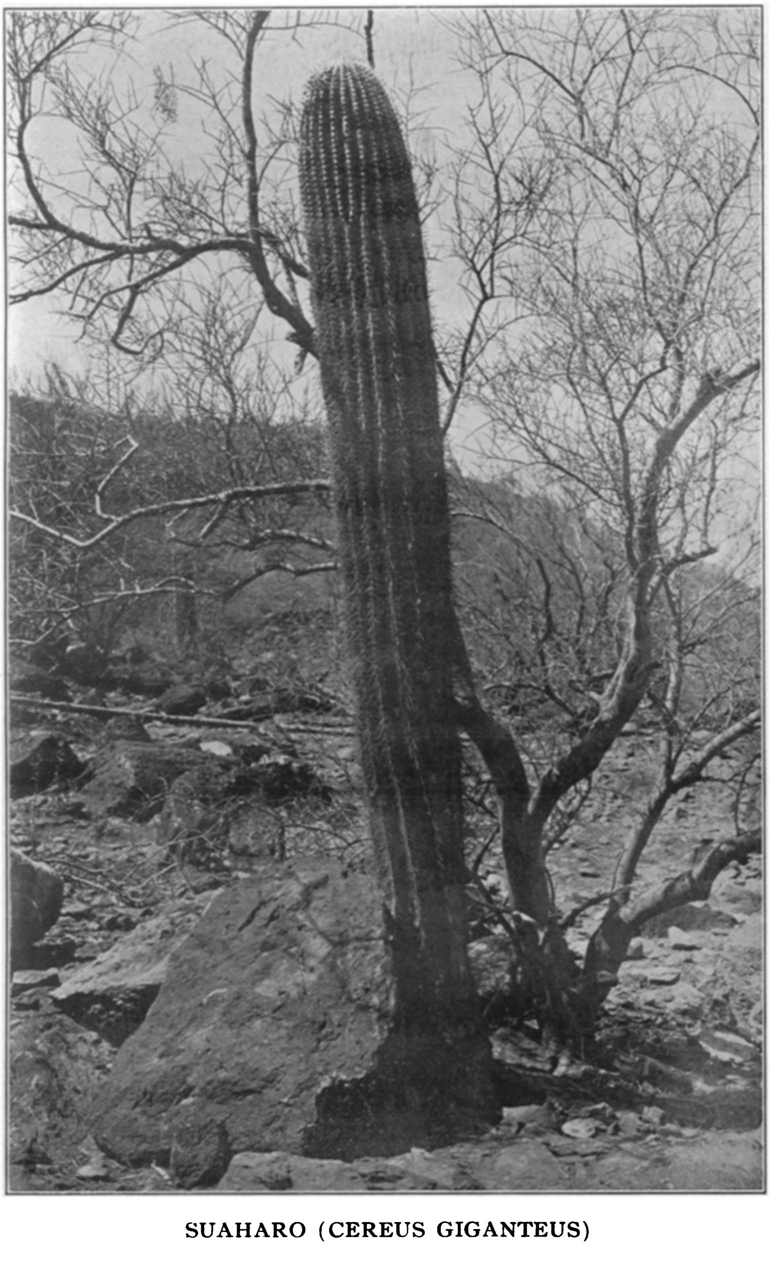
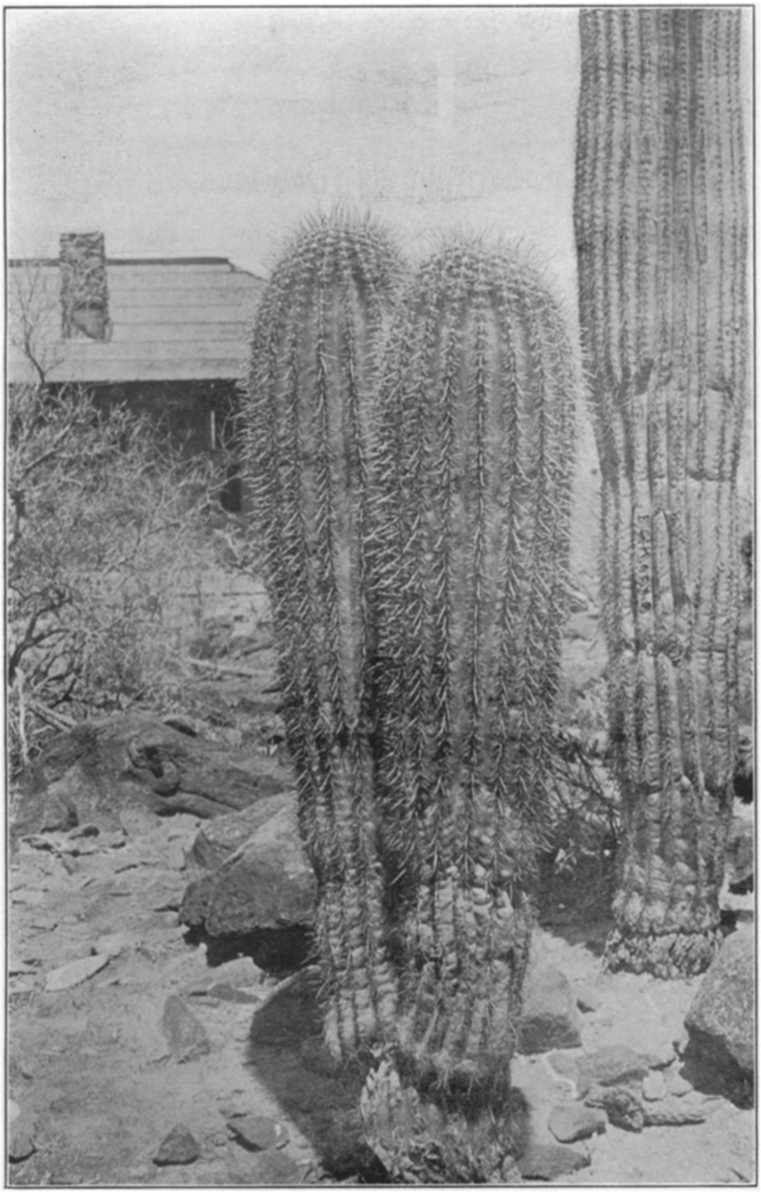
Description of plates 3 and 4

PLATE 3. Suaharo number 1. Plant about 12 feet high, marked for observation about half way between base and apex.

PLATE 4. Suaharo number 4. A double-stemmed plant about six feet high, showing the very frequent enlargement of the stem near the top.



SUAHARO (CEREUS GIGANTEUS)



SUAHARO (CEREUS GIGANTEUS)